EARLY SILURIAN SINACANTHS (CHONDRICHTHYES) FROM CHINA

by ZHU MIN

ABSTRACT. Histological study of new specimens of sinacanth fin spines from the Lower Silurian of the north-western margin of the Tarim Basin (Xinjiang, China) shows that they have the same histology as the fin spines of chondrichthyans. On this basis it is argued that sinacanths are one of the oldest known chondrichthyans, rather than acanthodians, and their spines are the oldest known shark fin spines. Previous studies on sinacanths are critically reviewed. The family Sinacanthidae is erected to include *Sinacanthus* and its relatives with more than 15 fin spine ridges per side. It is suggested that *Sinacanthus fancunensis* is synonymous with *S. wuchangensis*. A new sinacanth genus and species, *Tarimacanthus bachuensis*, from the Lower Silurian of Tarim and South China, is erected.

THE sinacanths are a middle Palaeozoic fish group, exemplified by *Sinacanthus wuchangensis* which was erected by P'an (1959, 1964) for isolated fin spines from the Guodingshan Formation (Silurian: Wenlock) of Wuhan, China (Text-fig. 1), and referred originally to Acanthodidae. Liu (1973) reported *Sinacanthus* in Ningguo, Anhui, China (Text-fig. 1). Since then, large numbers of sinacanth specimens, all of Silurian age, have been found in eight provinces of South China (P'an *et al.* 1975; Li 1980; Pan 1986*a*, 1986*b*; Zeng 1988; Text-fig. 1). They are a key element of the endemic Silurian vertebrate fauna of South China, and have also been significant in regional stratigraphical correlation (Pan 1986*b*).

Turner (1986) assigned to 'cf. *Sinacanthus*' some fin spines from the Lower Devonian of Australia, previously reported by Chapman (1917) and Talent and Spencer-Jones (1963). She indicated some doubt as to their acanthodian affinity, and suggested that they may have belonged to a shark akin to *Antarctilamna* Young, 1982. At the same time, fin spines from the Upper Silurian–Middle Devonian of Bolivia were considered to resemble *Sinacanthus* (Janvier and Suarez-Riglos 1986; Gagnier *et al.* 1988), and Gagnier *et al.* (1988) erected *Sinacanthus boliviensis*. Gagnier *et al.* (1988) placed *Sinacanthus* in Acanthodii (order and family undetermined), but suggested that *Sinacanthus* might be a chondrichthyan rather than an acanthodian. Because all of the fin spines were disarticulated and preserved mainly as external or internal moulds, there was no sound evidence to distinguish them from either chondrichthyans or acanthodians, and the systematic position of *Sinacanthus* and related forms remained unclear. In a recent study, Liu (1995, footnote on p. 94) doubted the presence of *Sinacanthus* in Australia and Bolivia, and returned to the traditional classification of sinacanths as acanthodians. I have had the opportunity to examine the Bolivian fin spines, currently housed in Paris (Muséum National d'Histoire Naturelle), and am able to confirm that both sinacanths and acanthodians are present in Bolivia. As to sinacanths in Australia, I follow Turner's (1986) proposal, based on the material illustrated by Talent and Spencer-Jones (1963) which shows similarities to the Chinese sinacanths.

The sinacanth material reported in this study was collected from the Silurian of the north-western margin of the Tarim Basin in 1992 by the author and his colleagues (Wang Junqing and Liu Shifan; Text-fig. 1, localities 11 and 12). Abundant fin spines, some galeaspids and large numbers of vertebrate microremains including dermal scale-units of galeaspids and scales of chondrichthyans indicate a diverse vertebrate fauna similar to the Llandovery–Wenlock vertebrate fauna of South China. This fauna was first reported from Tarim by Wang *et al.* (1988), and further investigated by

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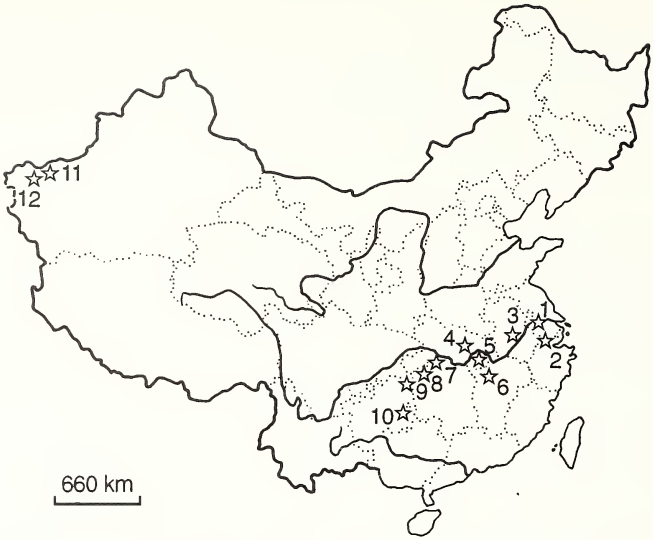

TEXT-FIG. 1. Sincanth localities in China. Dotted lines represent province boundaries. 1, Nanjing and Wuxi, Jiangsu; 2, Ningguo, Anhui, and Changxing, Zhejiang; 3, Chaoxian, Anhui; 4, Jingshan, Hubei; 5, Wuhan, Hubei; 6, Ruichang, Jiangxi; 7, Lixian, Hunan; 8, Dayong, Hunan; 9, Xiushan, Sichuan; 10, Kaili, Guizhou; 11, Kalpin, Xinjiang; 12, Bachu, Xinjiang.

Liu (1995) and Wang *et al.* (1996). The discovery of sinacanths in Tarim supports other evidence for biogeographical affinity between the South China and Tarim blocks in the Silurian (Liu 1993, 1995; Wang *et al.* 1996). The new sinacanth spines can be used to determine the systematic position of this group because, although disarticulated, like those from South China, they are composed of well preserved hard tissues and are suitable for histological research.

Resolution of the debatable systematic position of sinacanths, using histological details, will also help to classify the various fin spine species. In South China, five species (P'an 1959, 1964; Liu 1973; P'an *et al.* 1975), as well as several unnamed forms (Zeng 1988), have been referred to sinacanths. However, different types of fin spine found in the same bed, such as *Sinacanthus wuchangensis* and *S. triangulatus*, might represent different taxa if they are chondrichthyans, or may be better regarded as from the same fish if they are acanthodians. For this reason, the systematic revision of the sinacanths given below follows the discussion of the systematic affinity of sinacanths.

Institutional abbreviations. GM.V (Geological Museum of China, Beijing); HV (Regional Geological Surveying Team, Bureau of Geology and Mineral Resources of Hunan Province, Xiangtan); IVPP.V (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing); VF (Institute of Geology, Chinese Academy of Geological Sciences, Beijing).

HISTORICAL REVIEW OF STUDIES OF SINACANTH

Sinacanthus was erected by P'an (1959), with one species (*S. wuchangensis*) described briefly on the basis of two incomplete fin spines (P'an 1959, pl. 4, figs 3–4). However, no holotype was designated, so the two specimens must be considered as syntypes. Together with these two fin spines, a fragment of the headshield of *Hanyangaspis* (P'an *et al.* 1975) was found. This was first referred to the antiarchs by P'an (1959), but is in fact the first galeaspid to be figured from China (P'an 1959, pl. 5, fig. 7; cf. Liu 1965). In addition, the citation date of *Sinacanthus* and *S. wuchangensis* should be 1959 according to the International Code of Zoological Nomenclature (Ride *et al.* 1985, Article 22), rather than 1957 (P'an 1959, 1964; P'an *et al.* 1975; Turner 1986; Gagnier *et al.* 1988; Liu 1993, 1995).

P'an (1964) published a more formal study of *Sinacanthus* and *S. wuchangensis*, based on new material from the type locality (Wuhan, China). He also designated a holotype (P'an 1964, pl. 1, fig. 1a–b; see also P'an 1959, pl. 4, fig. 3) and a paratype (P'an 1964, pl. 1, fig. 2a–b) of *S. wuchangensis*. However, since both holotype and paratype should be fixed in the original publication (Ride *et al.* 1985, Article 73), the holotype of P'an (1964) should be regarded as the lectotype of *S. wuchangensis*, and his paratype as the paralectotype.

A second species of *Sinacanthus* (*S. fancunensis*) was described from Ningguo, Anhui, China (Text-fig. 1) by Liu (1973), but it is argued below that this species is synonymous with *S. wuchangensis*. P'an *et al.* (1975) described a third species of *Sinacanthus* (*S. triangulatus*) and a second sinacanth genus (*Neosinacanthus*) from the type locality of *S. wuchangensis*. Since then, sinacanths have been found to be widely distributed in South China (Li *et al.* 1978; Xia 1978; Pan 1984, 1986*a*, 1986*b*; Pan and Dineley 1988; Zeng 1988; Text-fig. 1).

Regarding the age of sinacanths from South China, P'an (1959) first proposed a mid Devonian age for *S. wuchangensis*, but later (1964) modified this opinion to Devonian or older, while Liu (1973) regarded the age of *S. fancunensis* as Early Devonian. P'an *et al.* (1975) also adopted an Early Devonian age for *S. wuchangensis*, *S. triangulatus* and *Neosinacanthus planispinatus*. The Early Devonian age of *Sinacanthus* and *Neosinacanthus* has been generally accepted (Hou 1978; P'an *et al.* 1978; Xia 1978), although some have argued for an older, mid Silurian age (Li *et al.* 1978). More recently, evidence from invertebrate fossils and stratigraphical sequences has supported a Silurian age for the sinacanths (Li 1980; Wang *et al.* 1980; Lin 1982; Yang and Rong 1982), a view now supported by previous proponents of an Early Devonian age (Pan 1986*a*, 1986*b*; Liu 1995). To summarize, sinacanths are recorded only from the Llandovery to Wenlock of South China (Pan 1986*a*, 1986*b*; Pan and Dineley 1988; Zeng 1988; Liu 1995). Reports by Turner (1986), who assumed a Silurian–Early Devonian age for *Sinacanthus* in South China, and Janvier and Suarez-Riglos (1986), who state that *Sinacanthus* is known from the Lower and Middle Devonian of China, are incorrect.

SINACANTH HISTOLOGY

It is generally difficult to distinguish between disarticulated ridged fin spines of acanthodians and chondrichthyans. However, they exhibit obvious differences in histological structure. In acanthodians, the fin spines usually consist of three layers: superficial, middle, and basal. In some mature fin spines, a central cavity osteon or denteon may fill in the central cavity (Denison 1979). The superficial layer (also referred to as the sculpture layer) forms the ridges of the fin spine. This layer, composed of orthodentine or mesodentine (Ørvig 1967), is distinguished histologically from the underlying middle layer, which is formed of either cellular bone or trabecular dentine (Ørvig 1967). When present, the basal layer lining the central cavity is composed of cellular bone or dentine. Enamel or enameloid tissue has not been identified in the fin spines of acanthodians. Amongst chondrichthyans, only some fossil sharks, such as *Ctenacanthus* Maisey, 1981, *Antarctilamna* Young, 1982 and *Tristychius* Zangerl, 1981, have ridged fin spines. These fin spines consist of two layers and, in some specimens, a thin enamel layer on the surface. Internally, a thin basal layer lines the central cavity, as in acanthodians. This inner layer is formed of lamellar dentine

(Maisey 1975). The outer layer, composed of trabecular dentine, forms the ridges and trunk of the fin spine. Thus, the hard tissue forming the fin spine ridges in chondrichthyans is trabecular dentine, whereas in acanthodians it is orthodentine or mesodentine. Therefore, the identification of the hard tissue forming the fin spine, especially that of the ridges, is essential for the determination of the systematic affinity of disarticulated fin spines.

Four thin sections show the histological structure of sinacanth fin spines. Two are cross sections of fin spines (Text-figs 3F, 4C), which are oval in form and very compressed. IVPP.V11249 was sectioned near the base (a–a′, Text-fig. 3D), where the posterior wall is open, and has a width/height index of nearly 6·00 (Text-fig. 3F). IVPP.V11250 was sectioned near the apex of the fin spine (a–a′, Text-fig. 4B), where it is completely enclosed, and has a width/height index of about 5·00 (Text-fig. 4C). In both examples, the spine wall is fairly thin, and there is a relatively large central cavity (c.cav, Text-figs 3F, 4C). A thin compact layer, consisting of lamellar dentine (lam, Text-figs 3F, 4C; Pl. 1, fig. 1), lines the central cavity. It resembles the inner dentinous layer of fin spines from spinate sharks (Maisey 1975, 1979; Young 1982), or the basal layer in the fin spines of some acanthodians (Gross 1947; Denison 1979). Covering the inner lamellar layer is a zone of trabecular dentine (tra, Text-figs 3F, 4C; Pl. 1, fig. 1), which forms the main body of the fin spine, and is penetrated by many vascular canals. This outer layer extends into the ridges, whose tissue is thus homogeneous with that immediately beneath them. The trabecular dentine in the ridges is also pierced by vascular canals, although they are less numerous than those in the main body of the fin spine. No enameloid or enamel tissue was found on the surface of the ridges, or in the grooves between the ridges. Enameloid or enamel tissue is present in some, but not all, fin spines of spinate sharks (Maisey 1981, 1982; Young 1982).

SYSTEMATIC POSITION OF SINACANTHS

Evidence supporting the chondrichthyan affinity of sinacanths is as follows.

1. The tissue in the fin spine ridges is trabecular dentine and is the same as the tissue beneath the ridges. This pattern of hard tissue distribution is only found in the fin spines of some fossil chondrichthyans. In acanthodians, the tissue in the fin spine ridges is orthodentine or mesodentine, and is different from the cellular bone or trabecular dentine beneath the ridges.
2. Sinacanth fin spines from China and Australia (Talent and Spencer-Jones 1963) always lack an inserted base. This is also the case for most sinacanths from Bolivia (Janvier and Suarez-Riglos 1986; Gagnier *et al.* 1988), and this feature is too common to be attributed to loss due to preservation. The absence of a base may be plesiomorphic for chondrichthyans, by comparison with the short base in the fin spine of *Antarctilamna* (Young 1982). Thus, the short base of insertion in *Sinacanthus boliviensis* (Gagnier *et al.* 1988, fig. 8B–C) is likely to be derived, compared with other sinacanths.
3. The fin spines of sinacanths have numerous ridges, always more than 15 per side and reaching up to 50 per side (Zeng 1988). A large number of ridges is also commonly seen on the dorsal fin spines of sharks (Maisey 1981, 1982; Young 1982). By contrast, the ridges on acanthodian fin spines are generally few in number, although some climatiids have up to 15 ridges per side.

This distinction permits reassessment of some problematical fin spines. Janvier and Saurez-Riglos (1986) described a small fin spine associated with a scapulocoracoid from the uppermost Silurian of Bolivia. This fin spine is similar to *Sinacanthus* in its gross morphology (Janvier and Saurez-Riglos 1986, fig. 5C), but close examination shows that it has fewer than 15 ridges per side, as in other climatiids and is thus distinct from sinacanths.

Wang *et al.* (1980) erected a new acanthodian genus (*Neoasiacanthus*), represented by two species from the Fentou Formation (Wenlock) of Chaoxian, Anhui (Text-fig. 1). Pan (1986*b*) considered the spine specimens of *N. wanzhongensis* and *N. shizikouensis* to be placoderm spinal plates. Indeed, the holotype of *N. shizikouensis*, in which the posterior face opens almost to the apex of the spine (Wang *et al.* 1980, pl. 2, fig. 9c), closely resembles a placoderm spinal plate, and is distinct from the

acanthodian fin spine. For this reason, Pan's suggestion regarding the systematic position of *N. shizikouensis* is followed here. As to the type species of *Neoasiacanthus* (*N. wanzhongensis*), I still consider it to be an acanthodian. This species (Wang *et al.* 1980) has fin spines which are similar to those of sinacanths in their gross morphology and nodular ridges (Text-fig. 2G). However, since these fin spines have relatively few ridges (ten to thirteen ridges per side), *Neoasiacanthus* is more similar to acanthodians than to sinacanths. Similar fin spines have also been found in western Hunan (Zeng 1988, fin spine type 6), in association with sinacanth fin spines.

4. Faunal associations also support the chondrichthyan affinity of sinacanths. In Tarim, numerous chondrichthyan scales were found together with the sinacanth fin spines, but no acanthodian scales were obtained. Until now, no microvertebrate remains have been collected from the sinacanth-bearing beds of South China. In Bolivia, the sinacanth fin spines were also associated closely with abundant chondrichthyan remains (Janvier and Suarez-Riglos 1986; Gagnier *et al.* 1988, 1989; Janvier 1991).

The weight of evidence thus suggests that the sinacanths should be referred to the chondrichthyans, as provisionally suggested by Gagnier *et al.* (1988), rather than to the acanthodians as originally proposed. It should be emphasized that only fin spines with more than 15 ridges per side can be assigned to sinacanths, while those with fewer ridges are still considered as acanthodians. It might be argued that some sinacanth fin spines, such as *Neosinacanthus* (P'an *et al.* 1975), are quite broad at the base and short, and resemble the intermediate fin spines of acanthodians. However, the ornamented part of the fin spine is also broad and short in some chondrichthyans (Maisey 1982).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Family SINACANTHIDAE fam. nov.

Diagnosis. Elasmobranchs with tapering, strongly compressed dorsal fin spines; cross section from three to six times as long as wide; anterior face of fin spine acutely rounded, lateral face slightly convex or flat, posterior face concave and without a median ridge; spine wall fairly thin, leaving a large central cavity; spine surface marked with more than 15 longitudinal ridges and grooves; the number of ridges increases towards the base of the spine as a result of bifurcation and marginal insertion; ridges generally as wide as or wider than grooves; ridges with closely set or pectinated tubercles; tubercles of adjacent ridges never in contact; spine trunk and ridges composed of trabecular dentine; an inner layer of lamellar dentine is well developed; no enamel on the surface.

Remarks. Since the phylogeny of early elasmobranchs remains obscure, the diagnosis given above is more descriptive than phylogenetic. Some characters are also seen in other fin spines and may be plesiomorphic. The most characteristic features of sinacanths include the strongly compressed fin spine, its thin wall and large central cavity, more than 15 longitudinal ridges per side and the marginal insertion of ridges.

Sinacanth fin spines resemble those of the primitive elasmobranch *Ctenacanthus* (Maisey 1981) in their numerous longitudinal ridges ornamented with pectinated tubercles. However, *Ctenacanthus* differs from sinacanths in having tubercles of adjacent ridges almost touching (not in *C. specablis*), with a median ridge on the posterior face, and a cross section only twice to three times as long as it is wide. The marginal insertion of ridges is also absent, but this feature is seen along the posterior margin in *Sphenacanthus* (Maisey 1982). This form differs in the smooth or widely spaced nodular tuberculation of the ridges, and in having a cross section twice as long as it is wide. The marginal ridge insertion along the anterior margin seen in sinacanths is a kind of bifurcation, as was clearly shown in *Antarctilamna* (Young 1982).

Genus SINACANTHUS P'an, 1959

Type species. Sinacanthus wuchangensis P'an, 1959.

Diagnosis. Sinacanth with long and slender fin spines; spine gradually tapering, recurved posteriorly and dagger-shaped.

Sinacanthus wuchangensis P'an, 1959

Plate 1, figures 2–3, 6, 8; Text-figure 2A–E

1959 *Sinacanthus wuchangensis* P'an, p. 11, pl. 4, figs 3–4.
1964 *Sinacanthus wuchangensis* P'an, p. 142, pl. 1, figs 1–4.
p1973 *Sinacanthus fancunensis* Liu, p. 145, text-fig. 2a, pl. 1, figs 6–8 (*non* text-fig. 2b, pl. 1, fig. 5).
1988 Acanthodii indet. fin spine 5, Zeng, p. 291, text-fig. 2F, pl. 1, figs 10–11.
1995 *Sinacanthus wuchangensis* Liu, p. 88, text-fig. 1A, pl. 1, figs 1–6.
p1995 *Sinacanthus fancunensis* Liu, p. 89, text-fig. 1B, pl. 1, figs 7–8 (*non* text-fig. 1C, pl. 1, fig. 9).

Lectotype. An incomplete fin spine, MG.V1032a (Text-fig. 2A), designated as the holotype by P'an (1964); Wuhan, Hubei; Guodingshan Formation; Wenlock.

Syntypes. Two originally unnumbered fin spines (P'an 1959, pl. 4, figs 3–4). One (P'an 1959, pl. 4, fig. 3; Text-fig. 2A) later numbered as MG.V1032a, the other (P'an 1959, pl. 4, fig. 4; Text-fig. 2B) here numbered MG.V1032b.

Referred specimens. Fin spines described by P'an (1964, p. 143, pl. 1, figs 2–4; Text-fig. 2D–E) from the type locality; fin spines described by Liu (1973, p. 145, fig. 2a, pl. 1, figs 6–8; Text-fig. 2C) from Ningguo (Anhui); fin spine type 5, described by Zeng (1988, pp. 291–292, text-fig. 2F, pl. 1, figs 10–11) from western Hunan; IVPP.V12093-12100, described by Liu (1995, pp. 88–89, text-fig. 1A–B, pl. 1, figs 1–8) from Tarim; IVPP.V11247.1–4 (Pl. 1, figs 2–3, 6, 8) collected by the author and colleagues from Tarim.

Diagnosis. Species of *Sinacanthus* in which the fin spines have a short basal margin and more than 15 ridges per side.

Description. As is clearly shown by its syntypes (P'an 1959; Text-fig. 2A–B), *Sinacanthus wuchangensis* has a fairly slender, laterally compressed and gently tapering fin spine, whose ridges are ornamented by closely set tubercles, somewhat resembling those of *Ctenacanthus*. The ridges increase basally by means of bifurcation and marginal insertion. However, both types are fragmentary. The lectotype MG.V1032a (Text-fig. 2A) lacks the

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EXPLANATION OF PLATE 1

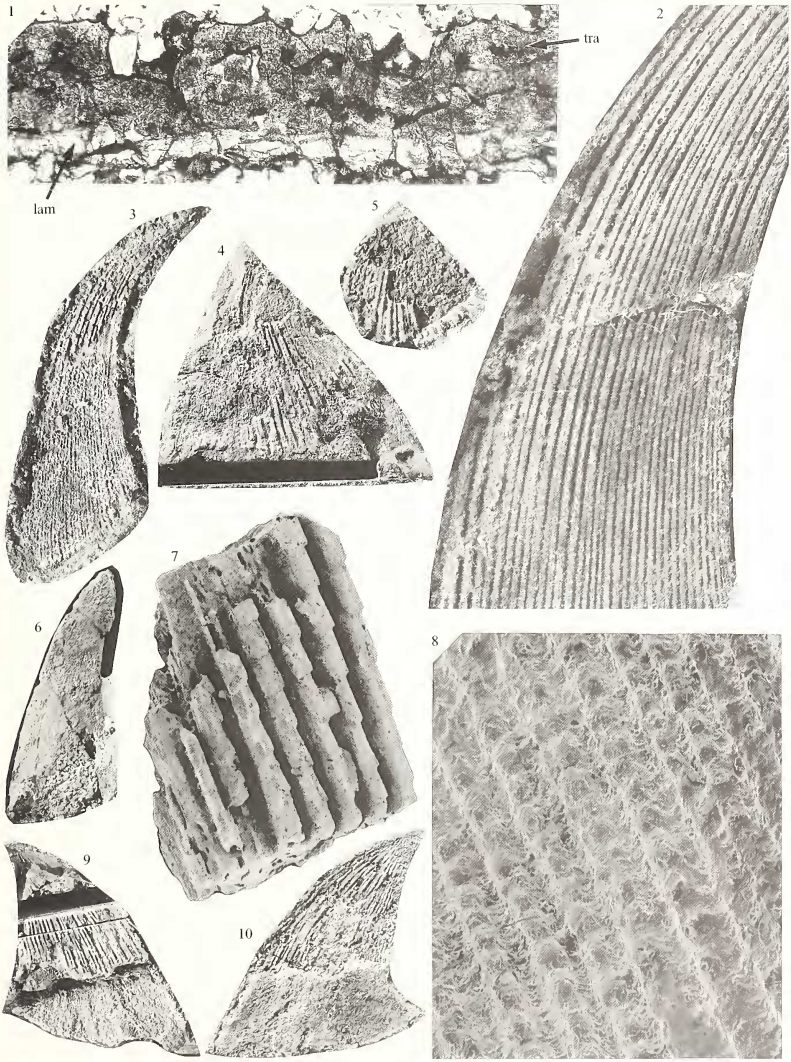
Figs 1, 4. *Neosinacanthus* sp. 2; IVPP.V11249; Tataaiertage Formation (Llandovery); Kalpin, Xinjiang, China. 1, cross section of the fin spine; × 60. 4, a fin spine; × 2. Abbreviations: lam, lamellar dentine; tra, trabecular dentine.

Figs 2–3, 6, 8. *Sinacanthus wuchangensis* P'an, 1959. 2, IVPP. V11247-1; an elastomere cast of the fin spine, showing bifurcation and marginal insertion of ridges; Tataaiertage Formation (Llandovery); Kalpin, Xinjiang; × 5. 3, IVPP.V11247-3; an elastomere cast of the fin spine; Yimugantawu Formation (Wenlock); Bachu, Xinjiang; × 2. 6, IVPP.V11247-4; an internal cast of the central cavity of a fin spine; Yimugantawu Formation (Wenlock); Bachu, Xinjiang; × 2. 8, IVPP.V11247-1; SEM photograph of an elastomere cast of the fin spine, showing ornamentation; Tataaiertage Formation (Llandovery); Kalpin, Xinjiang, China; × 30.

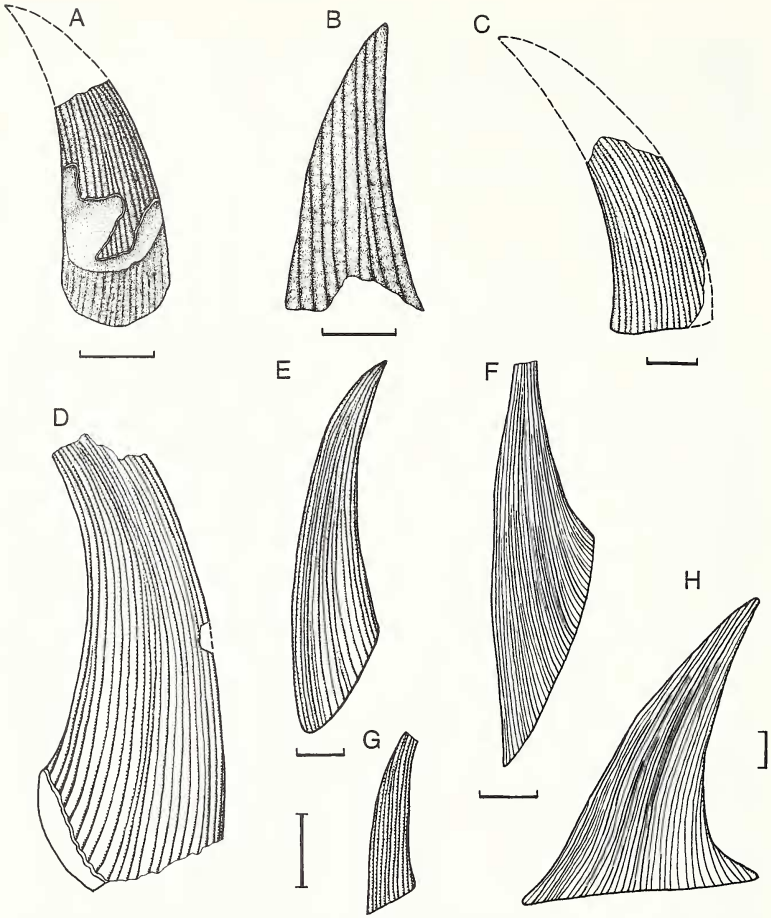
Fig. 5. *Neosinacanthus planispinatus* P'an and Liu, *in* P'an *et al.*, 1975; IVPP.V11248; a fin spine; Tataaiertage Formation (Llandovery); Kalpin, Xinjiang, China; × 2.

Fig. 7. Sinacanth; IVPP.V11252; SEM photograph of fin spine fragment, showing ornamentation; Yimugantawu Formation (Wenlock); Bachu, Xinjiang, China; × 45.

Figs 9–10. *Tarimacanthus bachuensis* gen. et sp. nov.; IVPP. V11250; a fin spine; Yimugantawu Formation (Wenlock); Bachu, Xinjiang, China; × 2.



ZHU, sinacanths



TEXT-FIG. 2. A–E, reconstruction of the fin spine of *Sinacanthus wuchangensis* P'an, 1959. A, lectotype, MG.V1032a (P'an 1959, pl. 4, fig. 3). B, one of the syntypes, MG.V1032b (P'an 1959, pl. 4, fig. 4). C, IVPP.V4412a (Liu 1973, pl. 1, fig. 7). D, MG.V1033 (P'an 1964, pl. 1, fig. 2a). E, MG.V1036 (P'an 1964, pl. 1, fig. 3). F, reconstruction of the holotype fin spine of *Sinacanthus triangulatus* P'an and Liu, *in* P'an *et al.*, 1975; MG.V1501 (P'an *et al.* 1975, pl. 10, fig. 4). G, reconstruction of the holotype fin spine of *Neoasiacanthus wanzhongensis* Wang, Xia and Chen, 1980; VF0262 (Wang *et al.* 1980, pl. 2, fig. 6). H, reconstruction of the fin spine of *Sinacanthus* sp.; HV006.1 (Zeng 1988, pl. 1, fig. 6). Scale bars represent 5 mm.

apical and basal extremities, and MG.V1032b consists only of the apical part (Text-fig. 2B). P'an (1964) assigned some more complete fin spines from the type locality to *S. wuchangensis*, and supplemented the original diagnosis. MG.V1033 (Text-fig. 2D), which was incorrectly designated as the paratype of *S. wuchangensis*, shows the addition of ridges by bifurcation and marginal insertion. MG.V1036 (Text-fig. 2E) is a complete fin spine, showing the relatively short basal margin of *S. wuchangensis*. IVPP.V4412a (Text-fig. 2C) is one of the syntypes of *S. fancunensis* (Liu 1973). As mentioned above, there are no significant differences between the types of *S. wuchangensis* and the slender fin spines of *S. fancunensis*.

Many fin spines of *S. wuchangensis* from Tarim are well preserved and fairly complete (Pl. 1, figs 2–3). They all lack the insertion base. The angle between the anterior and basal margins ranges from 50° to 90°. The fin spines are slender, laterally compressed, and recurved posteriorly at the apex. The fin spine wall is thin and encloses a relatively large central cavity (Pl. 1, fig. 6). The ornamentation of ridges is well shown in IVPP.V11247 (Pl. 1, figs 2, 8), and is same as that of the syntypes. SEM micrographs of some fragments of sinacanths from Tarim show detail of the tubercles on the surface of ridges. The ornamentation (Pl. 1, fig. 7) is similar to that seen in some species of *Ctenacanthus*, such as *C. littoni* (Maisey 1981).

Remarks. Liu (1973) established *Sinacanthus fancunensis* for fin spines from Anhui, but did not assign a holotype, so all the specimens in his study must be regarded as syntypes of *S. fancunensis*. Liu (1973) acknowledged that this species was very similar to the type species of *Sinacanthus*, but proposed two differences: the anterior and posterior margins of the fin spine of *S. fancunensis* are nearly parallel in the lower half, whereas those of *S. wuchangensis* converge gently over the whole spine, and there are *c.* 25–30 ridges per side in the middle part of the fin spine of *S. fancunensis*, but less than 20 in *S. wuchangensis*. Neither distinction was later supported by Liu (1995), who proposed two alternative differences between these species: (1) the fin spine of *S. fancunensis* is more slender than that of *S. wuchangensis*; (2) the angle between the anterior and basal margins is about 70° in *S. wuchangensis* and close to 90° in *S. fancunensis*. However, these two differences are difficult to apply in practice, and are in my opinion invalid. Some fin spines referred to *S. wuchangensis* by Liu (1995), such as IVPP.V12094 (Liu 1995, pl. 1, fig. 2), are as slender as those referred to *S. fancunensis* by Liu (1973, 1995). In addition, the angle between the anterior and basal margins of the fin spine ranges between 70° and 90°, and is more probably due to individual variation rather than any specific significance. There are no definite differences between the slender fin spines of *S. fancunensis* and *S. wuchangensis*, hence *S. fancunensis* should be regarded as a junior synonym of *S. wuchangensis*. The 'intermediate fin spines' of *S. fancunensis* (Liu 1973, 1995) should be referred to a new sinacanth (as discussed below).

Fin spines of *S. boliviensis* (Gagnier *et al.* 1988) are quite similar to those of *S. wuchangensis* in outline and ornamentation, but differ in the possession of a short insertion base.

The Australian specimens referred to as 'cf. *Sinacanthus*' by Turner (1986) much resemble *S. wuchangensis* in their slender shape and numerous nodular ridges (Talent and Spencer-Jones 1963). They also lack an insertion base, as suggested by Turner (1986). They differ from *S. wuchangensis* in their straighter configuration and in the addition of ridges by intercalation as well as bifurcation and marginal ridge insertion. Therefore, they probably belong to a different species of *Sinacanthus*, *S. micracanthus* (Chapman, 1917).

Sinacanthus triangulatus P'an and Liu, *in* P'an *et al.*, 1975

Text-figure 2F

1975 *Sinacanthus triangulatus* P'an and Liu, *in* P'an *et al.*, p. 164, pl. 10, fig. 4.

Holotype. MG.V1501, a complete fin spine (P'an *et al.* 1975, pl. 10, fig. 4; Text-fig. 2F); Wuhan, Hubei; Guodingshan Formation; Wenlock.

Diagnosis. Species of *Sinacanthus* in which the fin spine has a very broad basal margin forming an acute angle (about 30°) with the anterior margin. There are up to 50 ridges per side near the base.

Remarks. This species is referred to *Sinacanthus* because of the slender and recurved shape of the fin spine (Text-fig. 2F). It differs from other species of *Sinacanthus* in the acute angle between the

anterior and basal margins of the fin spine. In addition, the basal margin is as long as the posterior margin of the spine.

Sinacanthus sp.

Text-figure 2H

1988 Acanthodii indet. fin spine 4, Zeng, p. 290, text-fig. 2D, pl. 1, fig. 6.

Referred specimens. Fin spines described by Zeng (1988) as 'fin spines 4', HV006.1–26; Dayong, Hunan; Rongxi Formation; Llandovery.

Remarks. This kind of fin spine (Text-fig. 2H) represents a new species of *Sinacanthus*, diagnosed as '*Sinacanthus* with a fin spine whose basal extremity is anteroposteriorly extended'. These fin spines exhibit the main characters of *Sinacanthus*: numerous nodular ridges (30–35 ridges per side at the base of the fin spine), the addition of ridges by marginal insertion and bifurcation, and a slender and posteriorly recurved configuration. They differ from *S. triangulatus* in that the basal margin is shorter than the posterior margin. In addition, the angle between the anterior and basal margins in this unnamed species is about 45°, and thus larger than that in *S. triangulatus* where it is about 30°.

Genus NEOSINACANTHUS P'an and Liu, *in* P'an *et al.*, 1975

Type species. Neosinacanthus planispinatus P'an and Liu, *in* P'an *et al.* 1975.

Diagnosis. Sinacanth with broad fin spine; anterior and posterior margins are straight.

Remarks. This genus is distinguished from other sinacanths by the straight anterior and posterior margins of the fin spine.

Neosinacanthus planispinatus P'an and Liu, *in* P'an *et al.*, 1975

Plate 1, figure 5; Text-figure 3A, C

1975 *Neosinacanthus planispinatus* P'an and Liu, *in* P'an *et al.*, p. 165, pl. 10, fig. 5a–b.
1988 Acanthodii indet. fin spine 2, Zeng, p. 290, text-fig. 2B, pl. 1, fig. 13.

Holotype. MG.V1502, a complete fin spine (P'an *et al.*, 1975, pl. 10, fig. 5a–b; Text-fig. 3A); Wuhan, Hubei; Guodingshan Formation; Wenlock.

Referred specimens. Fin spines described by Zeng as 'fin spines 2' from the Rongxi Formation (Llandovery) of Dayong, HV005.1–3 (Text-fig. 3C); a fin spine from Tarim, IVPP.V11248 (Pl. 1, fig. 5).

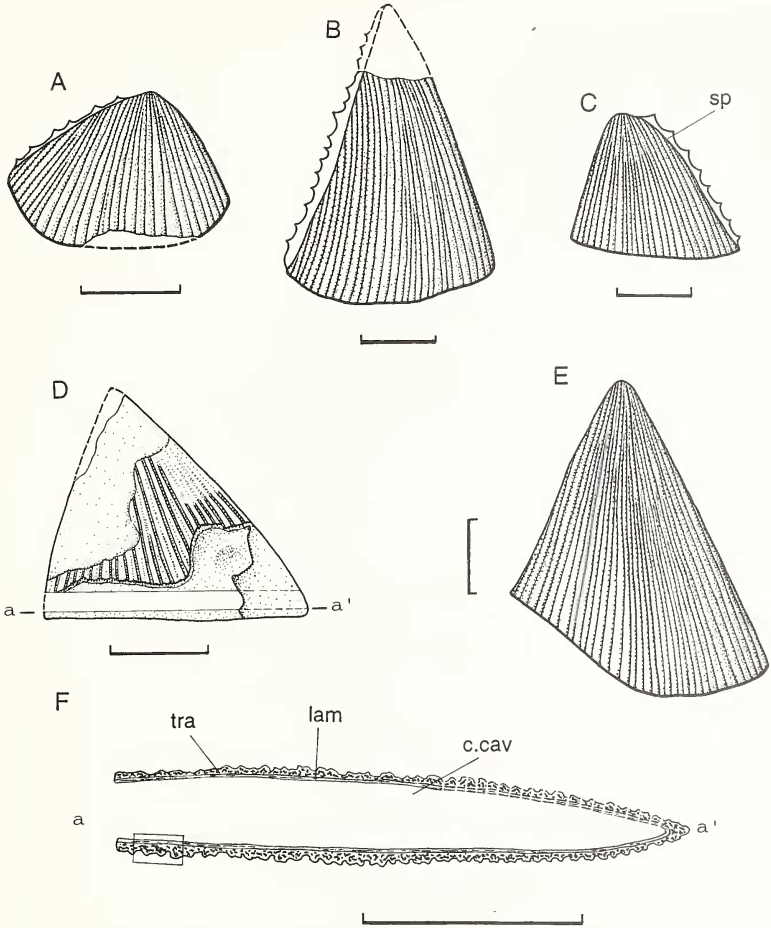
Diagnosis. Species of *Neosinacanthus* in which the fin spine is wider than long; the angle between anterior and posterior margins is greater than 70°; and the posterior margin is armed with small triangular denticles.

Remarks. The specimens from Hunan (Text-fig. 3C) and Xinjiang (Pl. 1, fig. 5) are slightly different from the holotype (Text-fig. 3A). The angle between the anterior and posterior margins reaches 90° in the holotype, and is evidently larger than that in the Hunan and Xinjiang specimens. However, this difference may reflect individual variation. The discovery of *Neosinacanthus planispinatus* in Xinjiang (Tarim) represents another element common to the Tarim and South China faunas during the Silurian (cf. Liu 1993).

Neosinacanthus sp. 1

Text-figure 3B

1988 Acanthodii indet. fin spine 1, Zeng, p. 289, text-fig. 2A, pl. 1, fig. 1.



TEXT-FIG. 3. *Neosinacanthus* P'an and Liu, *in* P'an *et al.*, 1975. A, C, *N. planispinatus* P'an and Liu, *in* P'an *et al.*, 1975, reconstruction of fin spines. A, holotype, MG.V1502 (P'an *et al.* 1975, pl. 10, fig. 5a–b). C, HV005-1 (Zeng 1988, pl. 1, fig. 13). B, *N.* sp. 1, reconstruction of the fin spine, HV004-1 (Zeng 1988, pl. 1, fig. 1). D–F, *N.* sp. 2. D, sketch of the fin spine, IVPP.V11249, a–a′ indicates position of cross section. E, reconstruction of the fin spine, HV010-1 (Zeng 1988, pl. 1, fig. 12); F, cross section of the fin spine (D); the rectangle indicates the region figured in Plate 1, figure 1. Abbreviations: c.cav, central cavity; lam, lamellar dentine; tra, trabecular dentine. Scale bars represent 10 mm.

Referred specimens. Fin spines described by Zeng (1988) as 'fin spines 1', HV004.1–21; Dayong, Hunan; Rongxi Formation; Llandovery.

Remarks. Since these fin spines (Text-fig. 3B) are relatively broad, and have straight anterior and posterior margins, they are referred to *Neosinacanthus*. They are similar to the fin spines of *N. planispinatus* in having small triangular denticles along the posterior margin, but are distinguished from the latter by their shape: longer than broad.

Neosinacanthus sp. 2

Plate 1, figures 1, 4; Text-figure 3D–F

1980 *Sinacanthus* sp., Wang *et al.*, pl. 1, fig. 5.
1988 Acanthodii indet. fin spine 7, Zeng, p. 92, text-fig. 2G, pl. 1, fig. 12.

Referred specimens. Fin spines described by Zeng (1988) as 'fin spine 7' (Text-fig. 3E), HV010.1–3 (Rongxi Formation, Llandovery, Dayong, Hunan); a fin spine from the Fentou Formation (Wenlock) of Chaoxian, Anhui; a fin spine from the Tataaiertage Formation (Llandovery) of Kalpin, Xinjiang (Tarim), IVPP.V11249 (Pl. 1, figs 1, 4; Text-fig. 3D, F).

Remarks. This unnamed species of *Neosinacanthus* differs from other species of the genus in lacking triangular denticles along the posterior margin of the fin spine. Similarities to other species include the fairly broad shape (as broad as high), and the straight anterior and posterior margins.

Genus TARIMACANTHUS gen. nov.

Derivation of name. From the Tarim Basin, Xinjiang, China.

Type species. Tarimacanthus bachuensis sp. nov.

Diagnosis. Sinacanth with fin spine which tapers rapidly and recurves posteriorly; fin spine blunt and almost as wide as long.

Remarks. This new genus resembles *Sinacanthus* in its posteriorly recurved shape, but differs in outline. The fin spine of *Tarimacanthus* is much blunter than that of *Sinacanthus* and tapers very rapidly, whereas that of *Sinacanthus* tapers gently and has a slender configuration. *Tarimacanthus* differs from *Neosinacanthus* in its recurved anterior and posterior margins.

Tarimacanthus bachuensis sp. nov.

Plate 1, figures 9–10; Text-figure 4A–C

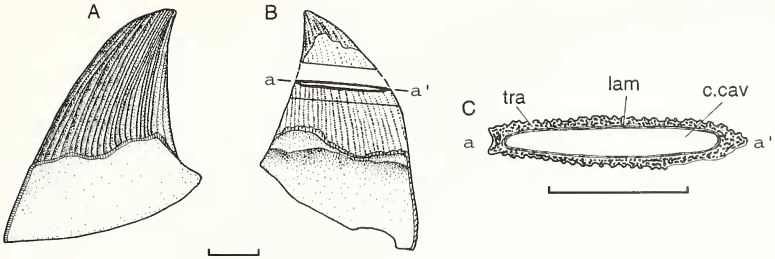
p1973 *Sinacanthus fancunensis* Liu, p. 145, text-fig. 2b, pl. 1, fig. 5 (*non* text-fig. 2a, pl. 1, figs 6–8).
1988 Acanthodii indet. fin spine 3, Zeng, p. 289, text-fig. 2C, pl. 1, figs 3–5.
p1995 *Sinacanthus fancunensis* Liu, p. 89, text-fig. 1C, pl. 1, fig. 9 (*non* text-fig. 1B, pl. 1, figs 7–8).

Derivation of name. From Bachu county, which is situated at the north-western margin of the Tarim Basin.

Holotype. A complete fin spine, IVPP.11250 (Pl. 1, figs 9–10; Text-fig. 4A–C); Bachu, Xinjiang; Yimugantawu Formation; Wenlock.

Referred specimens. A fin spine described by Liu (1973) from the Fentou Formation (Wenlock) of Ningguo, Anhui, IVPP.V4412d; fin spine type 3 described by Zeng (1988) from the Rongxi Formation (Landovery) of Dayong, western Hunan, HV009.1–7; IVPP.V12101, a fin spine described by Liu (1995) from the Yimugantawu Formation (Wenlock) of Bachu, Xinjiang.

Diagnosis. As for the genus. This is the only known species.



TEXT-FIG. 4. *Tarimacanthus bachuensis* gen. et sp. nov.; IVPP.V11250 (holotype); Llandovery, Tarim. A–B, sketches of the fin spine, a–a′ indicates position of cross section. C, cross section of the fin spine. Abbreviations: c.cav, central cavity; lam, lamellar dentine; tra, trabecular dentine. Scale bars represent 5 mm.

Description. The holotype is a complete fin spine with hard tissues preserved. It is posteriorly recurved and looks like the short beak of a bird. It is relatively broad and the width of the base is almost equal to the length of the fin spine. The fin spine is very compressed. In cross section, the fin spine is oval and much elongated, and about five times as deep as broad. The posterior surface is concave and very narrow, and no median ridge is visible. The wall is relatively thin and encloses a relatively large central cavity (c.cav, Text-fig. 4C) lined with a thin lamellar dentine (lam, Text-fig. 4C). This central cavity becomes larger ventrally. The trabecular dentine (tra, Text-fig. 4C) forms the ridges and trunk of the fin spine.

The lateral surface of the fin spine is slightly convex and is ornamented with numerous ridges, separated by narrow grooves. On the surface of the ridge are tubercles which are closely spaced. The number of ridges increases basally by bifurcation and marginal insertion. In the middle portion of the fin spine there are more than 22 ridges per side, reaching more than 30 ridges per side near the basal margin. The posterior margin lacks small triangular denticles.

Remarks. Liu (1973, 1995) identified two fin spines from Anhui and Xinjiang as the intermediate spines of *Sinacanthus*, since he considered the sinacanths as acanthodians, wherein the fin spines are variable. As sinacanths have been shown to be chondrichthyans, fin spines of different shapes presumably belong to different species. Therefore, a new genus and species is named for this distinctive type.

CONCLUSIONS

A critical review of sinacanth fin spines from the Lower Silurian of South China and Tarim has led to the identification of a new genus and species of sinacanth (*Tarimacanthus bachuensis*). Study of the histology of sinacanths shows that the hard tissue in the fin spine ridges is trabecular dentine, as is that in the fin spines of chondrichthyans. It is concluded on the evidence of morphology, faunal association and histology that sinacanths are chondrichthyans rather than acanthodians.

Until this study, the oldest known chondrichthyan scales came from the Llandovery of Siberia and Mongolia (Karatajute-Talimaa and Predtechenskyj 1995) and the oldest known chondrichthyan fin spines were from the Lochkovian of Wyoming, USA (Cappetta *et al.* 1993). Since the sinacanths are identified here as chondrichthyans and occurred as early as the Llandovery, they represent one of the oldest known groups of chondrichthyans and their fin spines are the oldest known shark fin spines.

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